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LETTER

Asynchronous demographic responses to Pleistocene climate change in Eastern Nearctic vertebrates

Frank T. Burbrink,^{1*} Yvonne L. Chan,² Edward A. Myers,^{3,4} Sara Ruane,⁵ Brian Tilston Smith⁶ and Michael J. Hickerson^{4,7,8}

Abstract

Pleistocene climatic cycles altered species distributions in the Eastern Nearctic of North America, yet the degree of congruent demographic response to the Pleistocene among codistributed taxa remains unknown. We use a hierarchical approximate Bayesian computational approach to test if population sizes across lineages of snakes, lizards, turtles, mammals, birds, salamanders and frogs in this region expanded synchronously to Late Pleistocene climate changes. Expansion occurred in 75% of 74 lineages, and of these, population size trajectories across the community were partially synchronous, with coexpansion found in at least 50% of lineages in each taxonomic group. For those taxa expanding outside of these synchronous pulses, factors related to when they entered the community, ecological thresholds or biotic interactions likely condition their timing of response to Pleistocene climate change. Unified timing of population size change across communities in response to Pleistocene climate cycles is likely rare in North America.

Keywords

Coexpansion, community, comparative phylogeography, hABC, historical demography, population genetics, refugia, temperate region.

Ecology Letters (2016)

INTRODUCTION

Populations respond to climate change in only a few ways. If species distributions are mostly determined by abiotic factors, then population size will expand and contract as favourable climate and habitat expands or contracts (Vrba 1992). Population sizes and ranges may also remain relatively static if they adapt to climate change (Jump & Peñuelas 2005), either by heritable adaptations or alterations in behaviour (Wong & Candolin 2015). If climate change alters interactions among species, some population sizes may be reduced dramatically or taxa may even locally go extinct, which would coincide with changes in range distribution and overall population size (Northfield *et al.* 2013; Barraclough 2015). The direction and extent of these responses are therefore defined by the ability of each species to adapt, migrate and tolerate interspecific interactions (Weinstock *et al.* 2006; Hofreiter & Stewart 2009; Jackson *et al.* 2014; Jackson & Blois 2015).

Dramatic climate change during the Quaternary caused entire communities to be displaced when massive ice sheets expanded and contracted (Davis 1983; Diamond & Case 1986). Historical demography related to climate change using population genetic techniques has been examined for many individual species (Avice 2000; Fontanella *et al.* 2008; Burbrink & Castoe 2009; Ruane *et al.* 2015), but it remains

unclear whether regional communities responded synchronously or asynchronously to the glacial cycles of the Pleistocene. Communities of species with similar physiological tolerances are predicted to respond to climate change as a cohesive unit (Hewitt 2000). However, previous research suggests that even closely related species in equivalent environments have expanded while others declined (Burbrink *et al.* 2008; Ruane *et al.* 2015), and similarly, models of population responses to future climate change scenarios predict that some species will expand while others will likely decline (Jump & Peñuelas 2005; Aitken *et al.* 2008; Bellard *et al.* 2012; Pearce-Higgins & Green 2014). Therefore, if taxa respond idiosyncratically to climate change and some species expand to occupy more areas whereas others decline, then entire communities should either move or disassemble (Blois *et al.* 2010; Jackson & Blois 2015).

The most recent, rapid and significant effect of global climate change occurred during the Quaternary, when ice sheets expanded and contracted altering both the environment and available land area. In the Eastern Nearctic (ENA), defined as the forested and coastal regions of the eastern USA, glacial advances beginning at ~ 2.59 Myr (Haug *et al.* 1999; Bartoli *et al.* 2005; Brierley & Fedorov 2010) extended as far south in the east to New York City and in the Midwest to south-central Illinois (Marshall *et al.* 2002; Gillespie *et al.* 2004).

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Temperature changed rapidly, in some cases at the scale of 5–10°C within several decades (Rahmstorf 2002), and glaciers advanced and retreated on 23, 40 and 100 kyr cycles altering biomes and communities (Hays *et al.* 1976). Associated with the action of glacial cycling, entire communities shifted, disappeared or reassembled rapidly in response to even minor variation within the timing of these Pleistocene glacial oscillations (Aitken *et al.* 2008; MacDonald *et al.* 2008; Jackson & Blois 2015).

In the ENA, the actions of the glaciers and associated environmental changes should have reduced population sizes and forced species into southern refugia proximal to present-day south-eastern North America as they tracked favourable climates (Avise 1992; Hewitt 2004; Waltari *et al.* 2007). After the glaciers receded and climate ameliorated, species had the opportunity to colonise newly available habitats at northern latitudes and increase population size (Ferris *et al.* 1999; Hewitt 2000). The magnitude of population size change therefore depends on the scale of the refugial areas and ability for species to expand into newly available and suitable habitat. The situation should be reversed in cases where species respond positively to glacial development and negatively to increasing temperatures, while responses may not be directly associated with changing climate or even occur at the same time. Furthermore, population sizes may also change in response to the invasion or exclusion of other taxa responding to environmental change (Tylianakis *et al.* 2008; McCluney *et al.* 2012) or periodic episodes of species-specific pathogens or other antagonists (Ricklefs 2015).

If species responded to glacially induced climate change, estimates of overall population size trajectories using genetic coalescent techniques should indicate expansion or decline throughout the Pleistocene (Avise *et al.* 1988; Drummond *et al.* 2005). Genetic studies in the ENA have documented population expansion, contraction and stasis (Burbrink *et al.* 2008; Fontanella *et al.* 2008; Tollis *et al.* 2012; Ruane *et al.* 2015), yet to date, there have been no tests to examine the timing of community-wide population responses due to Pleistocene climate change in this region. In western North America, the population ranges of small-mammal species in communities responded idiosyncratically to climate change just during the last century (Moritz *et al.* 2008). However, over longer time scales, population sizes among species with similar physiologies and habitat requirements should respond concertedly to glacial–interglacial climatic cycling (Lessa *et al.* 2003). In drastic climate change scenarios at deeper time scales, it remains unknown if the timing and trajectory of population size change is synchronous within communities (Fig. 1).

Despite difficulty associating population size change with the specific actions of a particular glacial cycle, it is possible to detect instances of concerted response to climate change given community-wide historical demographics (Chan *et al.* 2014; Xue & Hickerson 2015). Using a coalescent model that implements a hierarchical-approximate Bayesian computational (hABC) approach for detecting synchronous demographic change across communities (Chan *et al.* 2014), we characterise Pleistocene population demography across snakes, lizards, mammals, birds, turtles, salamanders and frogs in the ENA (Supporting Information). We determine if

population sizes within ENA communities expanded during the Pleistocene as predicted (Avise 1992; Hewitt 2004; Waltari *et al.* 2007). Using those taxa that show expansion, we estimate the degree of synchronicity among these populations and when taxon-specific pulses of expansion occurred. This study represents the first attempt to determine if population expansion within tetrapod groups in the ENA occurred synchronously relative to the glacial oscillations and climate change associated with the Pleistocene (Fig. 1).

METHODS AND MATERIALS

Datasets

We compiled mitochondrial DNA (mtDNA) sequences from 74 lineages of snakes, lizards, mammals, birds, turtles, salamanders and frogs among 58 species from GenBank (see Supporting Information) with 60% occupying ranges in formerly glaciated areas. We selected lineages from these taxa that were distributed almost exclusively in the ENA (Bailey 1995). We generated unbiased estimates of demography (Ho & Shapiro 2011) considering the Wright-Fisher model of an idealised population (Yang 2014), which assumes no geographical structure. Therefore, each lineage in our dataset did not contain multiple geographically monophyletic groups. We filtered out individuals or population structures that were distributed outside of the ENA. For species that exhibited multiple clades within the ENA, we split the datasets into separate lineages.

Although there are limitations of only using one mtDNA locus, the hABC model we employ accounts for the uncertainty associated with single-locus coalescent and mutational stochasticity while giving the benefit of ‘borrowing strength’ (Congdon 2001; Gelman *et al.* 2003) resulting from jointly analysing single-locus data for many species. This approach is analogous to greater statistical accuracy resulting from multi-locus inferences from a single species (Chan *et al.* 2014; Xue & Hickerson 2015). In the method used here, species are free to have independent demographic histories (i.e. effective population sizes, expansion magnitudes and expansion times) that are modelled through global hyperprior distributions.

Summary Statistics and Bayesian Skyline Plots

For each of the lineages, we obtained estimates of the parameter θ ($4N_e\mu$) and the following summary statistics: number of sites, number of transition/number of transversion, gamma, substitutions/generation, number of segregating sites, nucleotide diversity, number of haplotypes, haplotype diversity, Tajima’s D and the R_2 population growth test (Tajima 1989; Harpending 1994; Beaumont *et al.* 2002; Ramos-Onsins & Rozas 2002). We used BEAST v1.8.1 (Drummond *et al.* 2012) to generate Bayesian skyline plots (Drummond *et al.* 2005), which estimate changes in effective population size (N_e) over time. To parameterise these models, we scaled time with mutation rates in generation times for each group of vertebrate (Supporting Information) using the HKY model of nucleotide substitution and the coalescent Bayesian skyline tree prior where the number of groups was adjusted based on sample size, and a piecewise-constant skyline model. We used

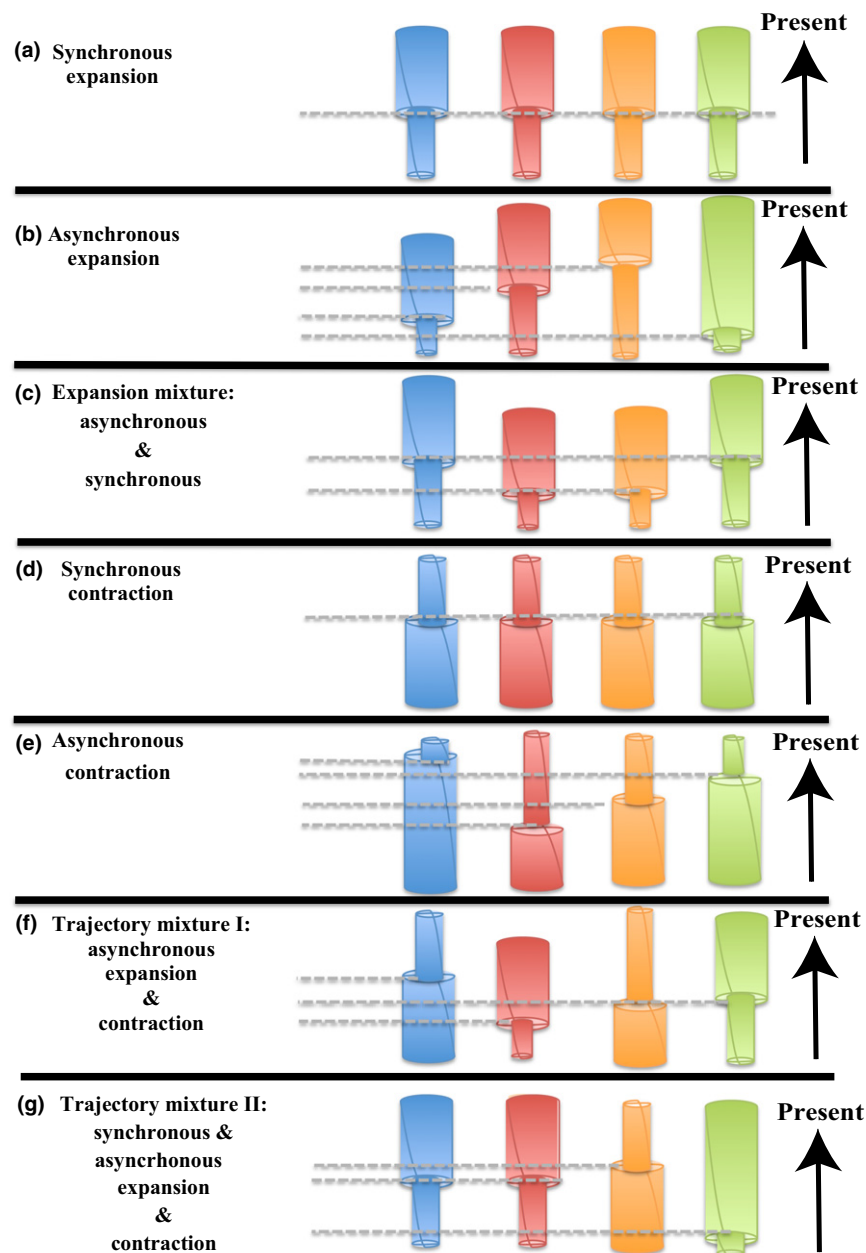


Figure 1 Schematic showing synchronous and asynchronous instantaneous expansion and contraction from the past to the present, where different taxa are represented by different colours and population size change is represented by the transition between small and large tubes. The grey dashed lines indicate the time when population sizes changed. In this study, we test models a–c.

a strict clock and specified a prior distribution on the clock rate to account for uncertainty in the mutation rate using a lognormal distribution with a standard deviation of 0.1, uniform or point estimate (Supporting Information). We ran each of these datasets for a minimum of 50 million generations sampling every 5000th generation to yield effective sample sizes (ESS) for all parameters >200 . Given the 95% credible intervals around median skyline plots, we estimated general trajectories of slopes (from a scale where the origin of the graph represents time 0 on the abscissa and current population size on the ordinate) as: (1) stable (not different from a slope of 0), (2) growing (negative slope) or (3) declining (positive slope). We further characterised these patterns visually to

determine if the general trajectories changed throughout the history of the lineage. From these slopes we determined if growth profiles differed among taxonomic groups using an ANOVA with a Bonferroni correction in R (R Core Team 2015). We also correlated these slopes with the non-genealogical estimates of expansion.

Modelling community-wide demographic responses

We used an hABC method in a multi-taxon statistical framework, which enables community-level inference while allowing demographic parameters to vary independently across taxa. To infer community dynamics from the aggregated mtDNA

datasets, we used the hABC approach developed by Chan *et al.* (2014) that estimates ζ , the proportion of taxa in a community sample that coexpanded at a time τ_s generations in the past. This hyperparameter index ζ ranges from 0.0 (completely asynchronous times of expansion across the community sample) to 1.0 (a synchronous expansion time across the entire community sample). For intermediate models, ζ is proportional to the number of species from a sample that coexpand synchronously with $1 - \zeta$ conversely being proportional to the number of species that expand at independent times.

Following Chan *et al.* (2014), for each of the n taxa, we used uniform priors for contemporary effective population sizes $N_i = \{N_1, \dots, N_n\}$, expansion magnitudes $\varepsilon_i = \{\varepsilon_1, \dots, \varepsilon_n\}$ and independent or synchronous expansion times ($\tau_i = \{\tau_1, \dots, \tau_{n(1-\zeta)}\}$ or τ_s), respectively). Specific priors included U (1–500 000 years) for τ_i and τ_s , U (5x – 20x) for ε_i , and lineage-specific U for each N_i (Supporting Information). Because ε and N can vary across taxa, we estimated ζ to determine how many taxa were in a single pulse of demographic expansion. Because ζ can be misleading as it does not necessarily correspond to the overall variability in expansion times, we also estimated the overall mean expansion time $[E(\tau)]$, the coexpansion time (τ_s) and the dispersion index of expansion times $[Var(\tau)/E(\tau)]$. Mutation rates were drawn from lineage-specific uniform priors (Supporting Information). As we are only estimating coexpansion proportions and time parameters, we filtered out datasets to exclude taxa that show contraction or stasis (Tajima's $D > 0$), or those with Bayesian skyline plots with positive or 0 slopes.

We used the program hBayeSSC (Chan *et al.* 2014; <https://github.com/UH-Bioinformatics/hBayeSSC>) to generate 200 000 simulated datasets per tetrapod group (1.46×10^7 simulated communities) based on sampling configurations identical to the observed data (i.e. number of individuals and sequence length, and locus type) and parameter values randomly drawn from the prior. For each tetrapod group, we calculated a vector D_i characterising the community-scale summary statistics (the mean, variance, skewness and kurtosis in the number of haplotypes, haplotypic diversity, nucleotide diversity and Tajima's D across lineages). Subsequently, the posterior distribution of the hyperparameters of interest (i.e. ζ , $E(\tau)$, τ_s and $Var(\tau)/E(\tau)$) was sampled using standard ABC rejection sampling using the C program msReject (<http://msbayes.sourceforge.net/>). The hyperparameter values for the posterior correspond to the datasets with the 500 smallest Euclidian distances between D_i and the observed summary statistic vector (D_* ; Chan *et al.* 2014).

We used PCA and histograms of the Euclidian distances between the observed and the 5000 closest simulated summary statistic vectors to verify that the model generated the main features of observed data. After finding that the mammal data poorly fit the model due to the high variance in the number of haplotypes across lineages, we removed this summary statistic in the mammal dataset.

Testing the influence of dispersal ability and expansion

We tested whether the variance in demographic histories among lineages could be explained by coarse-scale differences

in dispersal ability. We assigned each lineage to a locomotion type (crawling, walking, jumping or flight) that characterises how adults of each organism most frequently move across the landscape (Supporting Information).

We generated a phylogeny with a representative from each lineage ($n = 72$) to account for the non-independence of lineage locomotion type in subsequent comparative analysis. Only two species (*Pseudobranchius striatus* and *Apalone spinifer*) used swimming as their predominant locomotion type, thus we excluded them from further comparative analyses. To estimate a phylogeny, we downloaded the most commonly available homologous mtDNA loci (Cytochrome *b*; Cytochrome oxidase subunit I and NADH dehydrogenase subunit II) from each lineage in our dataset. In some cases homologous loci were not available for a lineage, therefore, we used a closely related taxon; when sequence data were unavailable for lineages with multiple populations in ENA, we grafted the tip onto the tree (see below). Because of the difficulty in aligning mtDNA sequence across clades at this level of divergence, we estimated phylogenies for each clade independently. We inferred a phylogeny for each clade using BEAST v1.8.1 (Drummond *et al.* 2012) using the following settings: GTR + G nucleotide substitution model, lognormal relaxed clock and Yule process speciation tree prior. For the ucl.d.mean prior, we specified a lognormal distribution with a mean and standard deviation of 1 (mean in real space) because we wanted to estimate relative branch lengths and not absolute time. For all other priors we used the default settings. We ran the tree for 50 million generations and thinned every 5000; stationarity assessed in TRACER v1.5 (Rambaut & Drummond 2007). We estimated the maximum clade credibility (MCC) tree from the posterior distribution of trees from each clade and grafted each MCC tree together, including missing phylogeographic lineages, to build a single tree using the bind.tree function and rescaled relative branch lengths in the R package ape (Paradis *et al.* 2004).

To broadly characterise the magnitude of N_e change in each lineage, we fit median N_e and time, obtained from the Bayesian skyline posterior distribution, to a linear model using the lm function in R (R Core Team 2015) to obtain the slope. We fit log-converted slope and locomotion type to a phylogenetic ANOVA (Garland *et al.* 1993) using the aov.phylo function (aov.phylo[slope~locomotion type, phylogeny, nsims = 100]) in the R package Geiger (Harmon *et al.* 2008). We also determined if slope had significant phylogenetic signal using a randomised test of Blomberg's K in Phytools (Blomberg *et al.* 2003; Revell 2012) and if tetrapod groups had significantly different slopes.

RESULTS

Historical demography

All parameters in the Bayesian skyline plot analyses attained ESS values >200 showing that the MCMC sampling had reached stationarity and, given error estimates, yielded historical demographic changes discernible as expanding, contracting or stable through time (Fig. 2). All expansion and contraction events occurred throughout the Pleistocene across all groups,

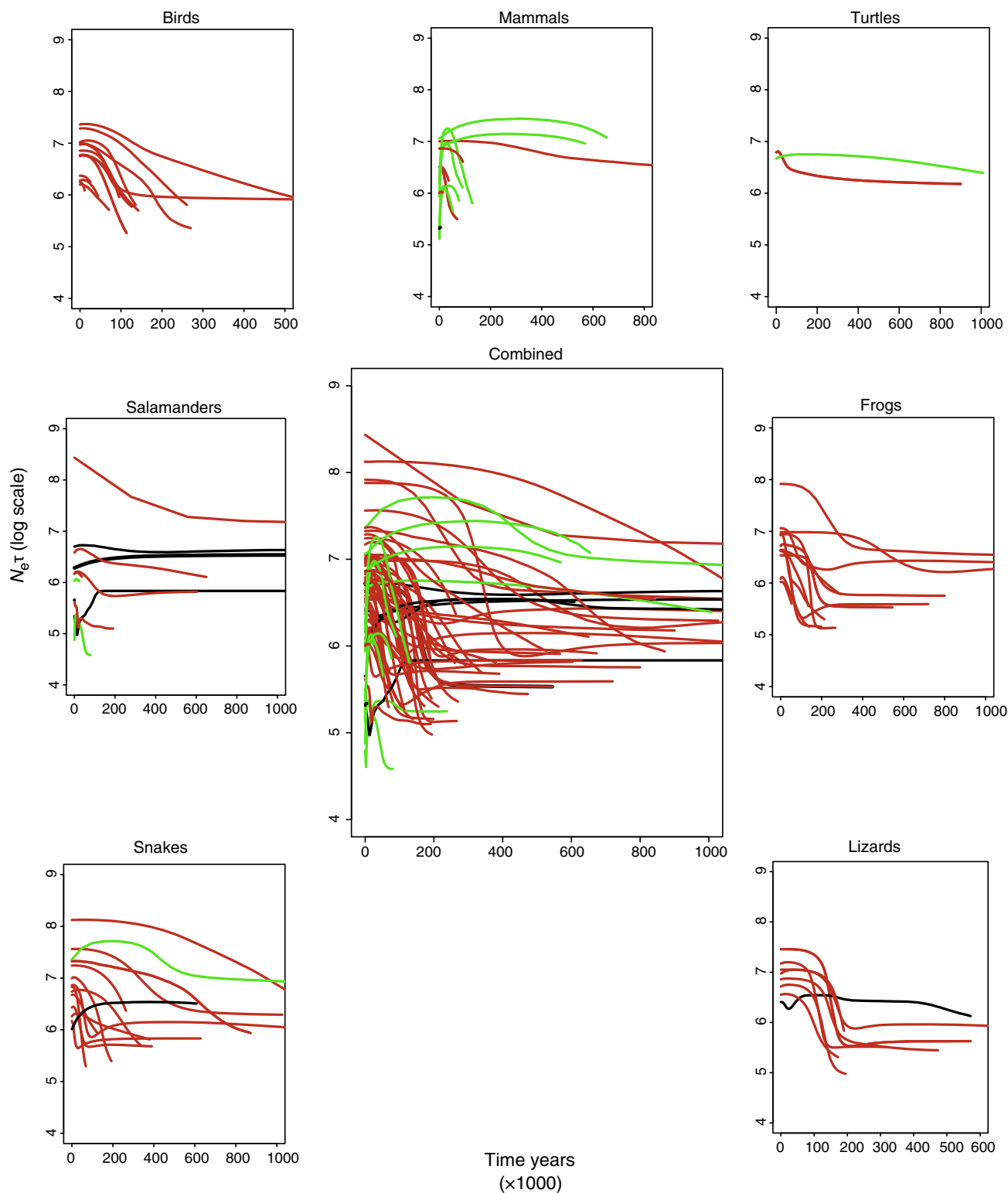


Figure 2 Combined Bayesian Skyline Plots showing expansion (red), expansion and contraction (green) and contraction (black) for each tetrapod group and combined groups scaled by the effective population size (N_e) and generation time (τ) and years ($\times 1000$).

although only 25% of the taxa showed some contraction. All metrics estimating population size change through time agreed; multiple coalescent measures (Tajima's D , R_2) were correlated with slopes estimated from BSP ($r = 0.352\text{--}0.444$; all $P < 0.001$; Supporting Information).

hABC tests of synchronous expansions

Before simulating population demographics of each tetrapod group, we determined that 10% of mammals, 0% birds, 50% of salamanders, 14% of snakes, 12.5% of lizards and 15% of

frogs did not show expansion. Therefore, along with the turtle taxa, which were too few, we excluded these lineages from the hABC analysis (Supporting Information).

Using the hABC procedure, we estimated ζ to be 0.75, 0.57, 0.50, 0.56, 0.75 and 0.62 in the six-taxon assemblages corresponding to snakes, lizards, salamanders, frogs, mammals and

birds, respectively (Fig. 3a). Comparing these with the dispersion index on expansion times (Fig. 3b) revealed consistent patterns. However, snakes showed an elevated dispersion index contrasting with the highest ζ estimate, which suggested that some outlier taxa expanded much earlier than the coexpansion pulse ($\tau_s = 49\,373$ ybp; Fig. 3c). This outlier likely

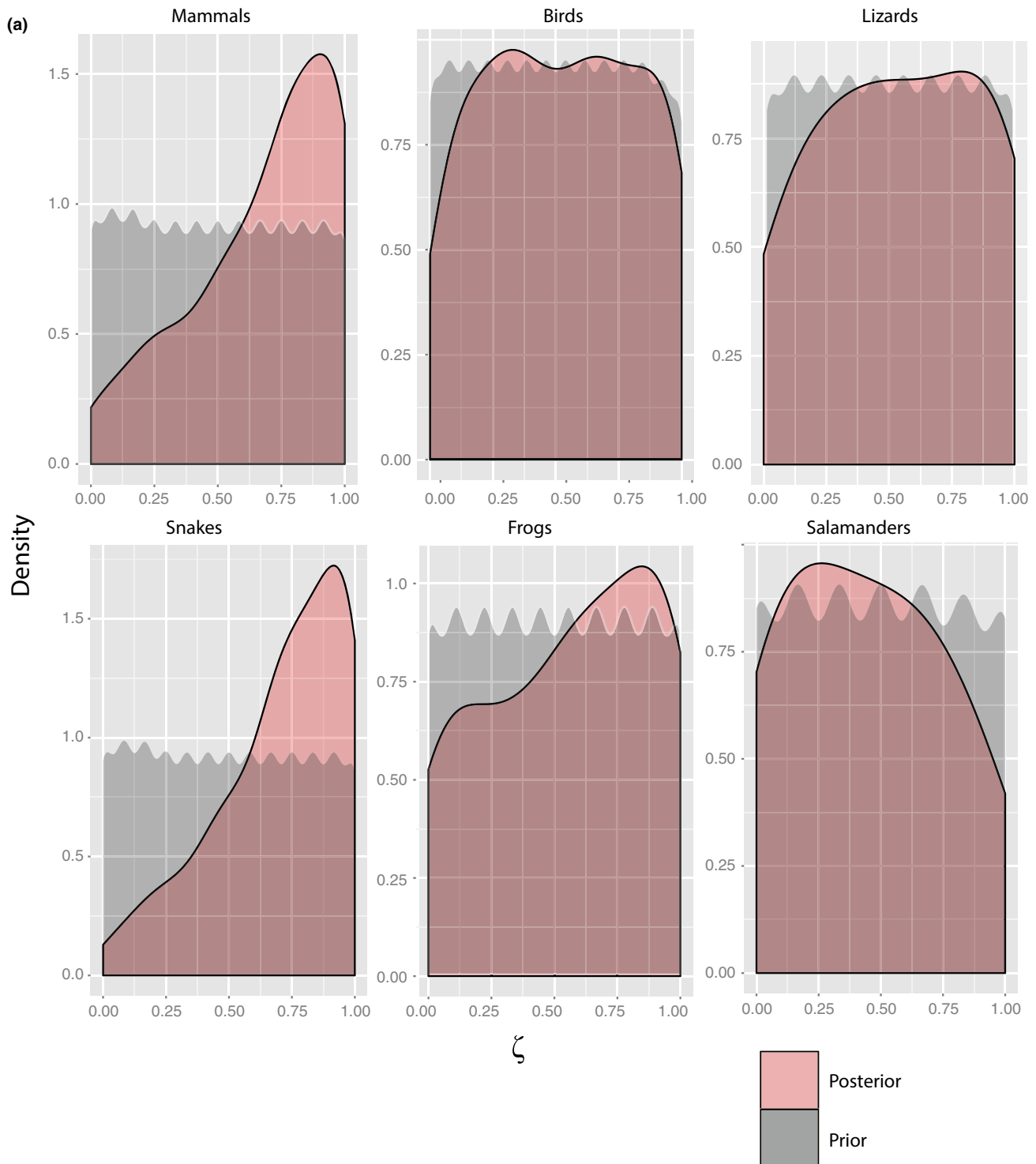


Figure 3 The outcomes of hierarchical approximate Bayesian computational modelling for coexpansion times for each vertebrate group where (a) is the frequency of coexpansion (ζ) priors and posteriors, (b) the dispersion index [$\text{Var}(\tau)/\text{E}(\tau)$] priors and posteriors and (c) the density distributions for synchronous expansion times (solid lines) and overall expansion times (dashed lines).

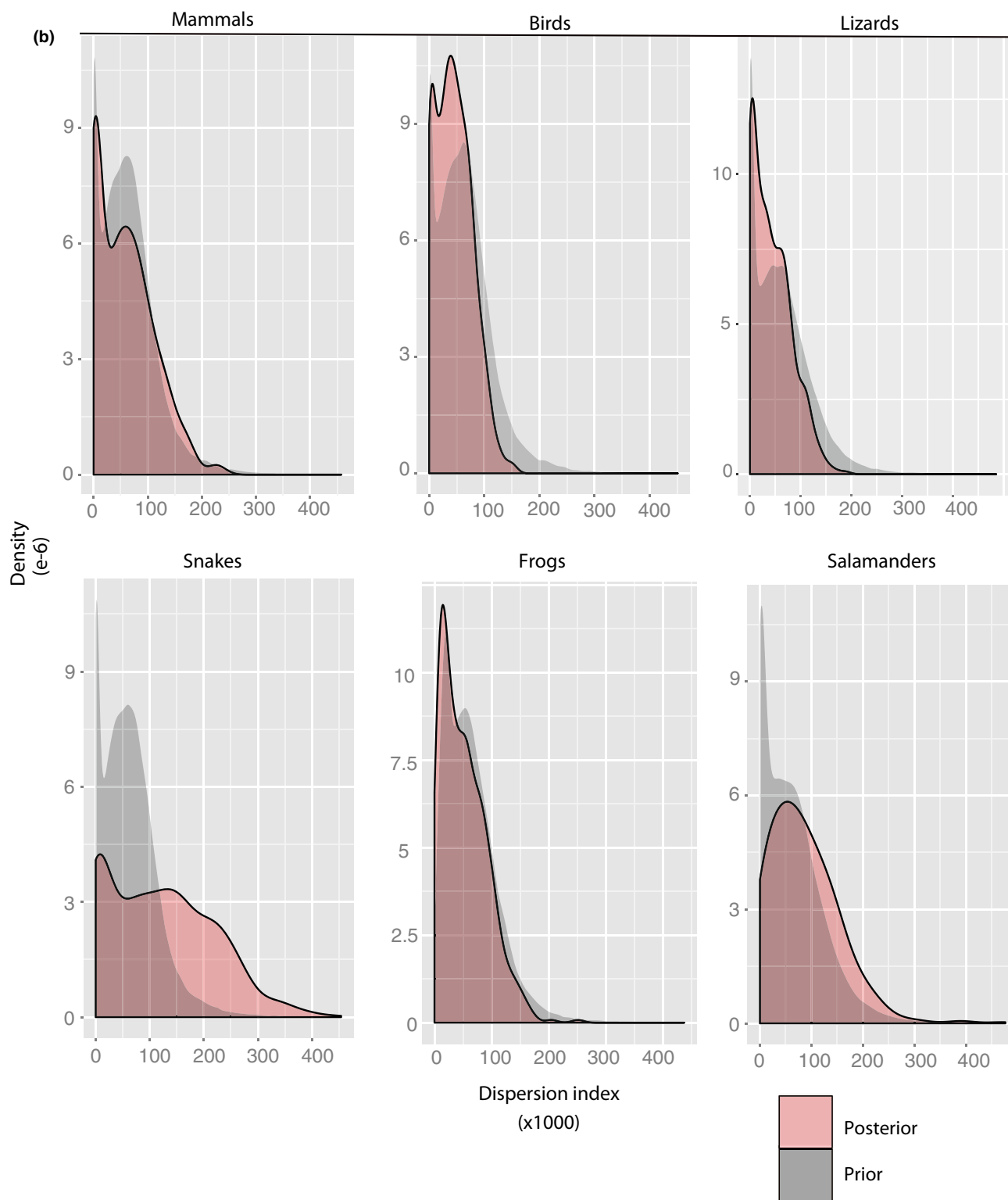


Figure 3 Continued.

corresponds to the Appalachian lineage of the ringneck snake (*Diadophis punctatus*; Fontanella et al. 2008), where their BSP suggests populations expanded in the mid-Pleistocene. Although mammals showed a strong pulse of coexpansion, as characterised by $\zeta = 0.75$, this group had the lowest dispersion index with only minor differences between coexpansion times and

overall mean expansion times (Fig. 3c), thereby suggesting that these mammal lineages had the strongest and most universal pulse of coexpansion, estimated at approximately 100 000 ybp.

These coexpansion pulses are estimated to have occurred in the Late Pleistocene in three of the assemblages (mammals, snakes and frogs; Fig. 3c). Mode estimates of coexpansion

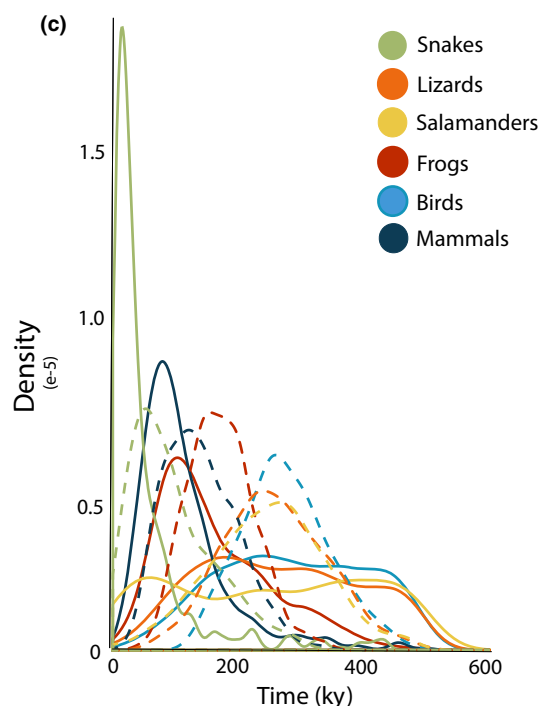


Figure 3 Continued.

times (τ_s) are 100 229 ybp, 49 373 ybp and 173 212 ybp for mammals, snakes and frogs, respectively (see Fig. 3c for the shape and extent of these distributions). In all three of these cases, the overall average expansion times $E(\tau)$ were older than the coexpansion times (114 764 ybp, 82 039 ybp and 174 805 ybp for mammals, snakes and frogs, respectively, see Fig. 3c for the shape and extent of these distributions). In contrast, mode estimates of coexpansion times for birds, salamanders and lizards corresponded to older dates of 310 468 ybp, 267 220 ybp and 269 034 ybp, respectively.

Dispersal ability and expansion

We found that the slopes of the BSPs were significantly different among locomotion types ($DF = 3$; F -value: 2.923; $Pr > F = 0.040$), with more mobile groups having steeper slopes, but this relationship was not significant when we accounted for phylogeny ($Pr > F = 0.871$). Similarly, while slope has significant phylogenetic signal (Blomberg's $K = 0.467$, $P = 0.001$), the six groups of tetrapods were not different after correction for phylogeny ($DF = 6$; F -value = 2.018; $P = 0.922$).

All genetic data, BSPs and hABC results are available via Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.c3q5c>.

DISCUSSION

The Eastern Nearctic underwent dramatic environmental change during the Late Pleistocene, where glaciers covered much of the region and altered both the abiotic and biotic environments (Comes & Kadereit 1998; Kleman *et al.* 2010).

Contrary to expectation, we do not find a uniform demographic response to climate change among community members. While trajectories of growth or decline were not shared among all species according to the BSP analyses, we find population expansion is the most common historical demographic trajectory in our ENA community sample (75%). Synchronous expansion was estimated in at least 50% of lineages within each group, indicating that both asynchronous and synchronous expansions are key factors influencing the assembly of communities through time. Mixed trajectories have been found among other organisms inhabiting the Nearctic (Lessa *et al.* 2003; Hewitt 2004; Guiher & Burbrink 2008; Tollis *et al.* 2012), although modelling the history of community-wide demographic responses regionally has been heretofore unattainable. All key expansion or contraction events were associated with the latter half of the Pleistocene where glaciers cycled every 100 kyr in relation to orbital eccentricity and not obliquity (41 kyr) or precession (23 kyr; Muller & MacDonald 1997). Moreover, pulses of coexpansion in mammals, snakes and frogs were estimated to be associated with younger dates. In particular, the coexpansion pulse of snakes perhaps coincided with the end of the Last Glacial Maximum (Raymo 1994; Bintanja & van de Wal 2008), the current interglacial where population size in many vertebrates, including humans, typically increased (Hewitt 2004). Also, our hABC parameter estimates [ζ , τ_s and $\text{Var}(\tau)/E(\tau)$] all point to a largely singular pulse of mammalian coexpansion dating to events that could have been associated with expansion after the penultimate glacial maximum, which is thought to have peaked approximately 140 kya (Colleoni *et al.* 2016). Obtaining precise times is often difficult given coalescent stochasticity from a single locus (Edwards & Beerli 2000; Wakeley 2008; Yang 2014), although the hABC method used here has been previously subjected to simulation-based cross validation and automatically accommodates the statistical uncertainty associated with using a single gene (Chan *et al.* 2014).

Given that the majority of all of our sampled species responded to change during the Late Pleistocene, the disparity in expansion synchronicity could have been due to selective sweeps on the mtDNA, bottlenecks or expansions in a subset of taxa resulting from subsequent glacial advances and retractions occurring thousands of years after earlier events affecting a larger proportion of taxa. Although genetic signatures should be dominated by the most recent demographic events (Yang 2014), our results contradict the standard paradigm of demographic expansion after the glaciers receded. However, considering the variability in physiologies, environmental preferences and interactions and life histories among these species, idiosyncratic demographic changes may not be unexpected.

Although we do recover clusters of early and late coexpansion, coexpansion among different taxonomic groups was not related to phylogeny, ecto- or endothermic physiology or locomotor type. For example, synchronous expansion occurred during the Illinoian or Wisconsin glacial periods among unrelated groups of both ectotherms and endotherms represented by mammals, snakes and frogs, whereas bird, lizard and salamander coexpansion pulses occurred prior to this in the Sangamonian Interglacial (Raymo 1994; Bintanja & van de Wal 2008; Fig. 3c). This finding suggests that the

ecological changes throughout different glacial cycles promoted major demographic shifts among different phylogenetic groups.

Importantly though, our results generate new questions regarding what combinations of synchronous and asynchronous expansion and contraction mean with respect to species assembly, species interaction and the putative effects of climate change on community disassembly. Not all species within a particular group expand (Fig. 2); at least 25% of the taxa in our dataset declined in the face of putatively similar ecological conditions throughout the Pleistocene. These declines were most noticeable in mammals, where continuous expansion was not common among the majority of taxa (Fig. 2). These opposite responses, therefore, suggest that conditions beneficial to some taxa were not to others or that biotic interactions affected declining taxa differently than expanding species (Gilman *et al.* 2010; Lurgi *et al.* 2012; Jackson & Blois 2015). Our study suggests that communities may not respond uniformly to future climate change. Similarly, considering individual responses to climate change in communities over the last century (Moritz *et al.* 2008) and unique spatial and temporal responses of species occurring in refugia (Stewart *et al.* 2010), modern communities would likely be disassembled as some taxa decline to extinction, whereas others expand to new regions and interact in novel ways with local taxa.

Our results imply complex changes in community composition over time, with synchronicity ranging from 50 to 75% of the expanding species per taxonomic group. This conservatively suggests that each of these pulses of coexpanding taxa responded at the same time to similar changing ecological conditions. The remaining asynchronous expansions did not occur at the same time and perhaps not even to similar types of ecological changes. If we consider that the timing and rate of expansion or contraction of populations directly relates to the ability for taxa to be present in greater or fewer communities in the ENA, respectively, then these asynchronous expansion times are consistent with trends in the fossil record where community composition is altered rapidly (Jump & Peñuelas 2005; Aitken *et al.* 2008; Bellard *et al.* 2012; Pearce-Higgins & Green 2014). In contrast, biogeographic processes related to dispersal in and out of communities could determine the degree of expansion synchronicity (Pigot & Etienne 2015). For example, asynchronous expansion may have occurred in those species that dispersed to the ENA earlier or later than the synchronously expanding groups. Alternatively, if all taxa were assembled prior to any expansion, asynchronicity would mean that some lineages require different ecological thresholds before expansion takes place (Bazzaz 1986; Jackson *et al.* 2009). It is also possible that asymmetric biotic interactions among taxa either enhance or retard the timing of expansion and colonisation (Cavender-Bares *et al.* 2009), thus reducing the propensity for coetaneous population growth.

Our results highlight several areas of exploration that connect processes related to demographic synchronicity with community assembly, biogeography and latitudinal diversity gradients. Expansion permits more species to occupy more areas geographically, whereas contraction may eliminate taxa entirely from local communities. Therefore, synchronously expanding species with the highest rate of growth should be

found in more areas, whereas lineages with populations historically in decline should not be abundant among the communities in the particular region of study. Taxa showing demographic expansion are also those likely to occur throughout the focal region and thus possess traits to colonise and remain in more communities even when facing potential competition (Cavender-Bares *et al.* 2009; Lavergne *et al.* 2010). It is also important to determine if asynchronicity is associated with different dispersal and community colonisation times. We did not model spatially explicit simultaneous expansion and contraction, although doing this would determine if similar ecological changes produce opposite demographic trends in related taxa. Also, it is possible that using only mtDNA here could bias synchronicity estimates given potential problems with single-locus estimates of historical events due to coalescent stochasticity and selection (Hurst & Jiggins 2005; Brito & Edwards 2009; Hung *et al.* 2013). Future research on historical community demography should include a greater representation of taxa from a community, sample the genome to reduce uncertainty (Xue & Hickerson 2015) and explore the signal of synchronous demographic change vs. synchronous genomic selection (Nosil & Feder 2013).

Finally, we suggest that the hABC models presented here may be useful for understanding latitudinal gradients in species diversity, which may be explained in part by higher rates of extinction towards the poles (Mittelbach *et al.* 2007). Currently, most studies working on diversity gradients use the fossil record or molecular phylogenies to estimate rates of speciation and extinction among regions, (Ricklefs 2003; McPherson & Jetz 2007; Pyron & Burbrink 2009), even though rates of extinction are known to be difficult to estimate (Rabosky 2010). If extinction is the main cause of latitudinal diversity asymmetries, then extant communities should produce a signal where asynchronous expansion and contraction occurs more often in temperate areas than the expected uniformly expanding or stable populations in tropical regions.

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AUTHORSHIP

FTB conceived the study, performed demographic analyses and wrote the first draft of the manuscript. EAM, SR and BTS collected data and performed demographic analyses. MH and YC performed hABC analyses. All authors contributed to editing and writing the manuscript.

DATA ACCESSIBILITY

All data and results available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.c3q5c>

REFERENCES

- Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. & Curtis-McLane, S. (2008). Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol. Appl.*, 1, 95–111.
- Avise, J.C. (1992). Molecular population-structure and the biogeographic history of a regional fauna - a case-history with lessons for conservation biology. *Oikos*, 63, 62–76.
- Avise, J.C. (2000). *Phylogeography: The History and Formation of Species*. Harvard University Press, Cambridge, MA.
- Avise, J.C., Ball, R.M. & Arnold, J. (1988). Current versus historical population sizes in vertebrate species with high gene flow - a comparison based on mitochondrial-DNA lineages and inbreeding theory for neutral mutations. *Mol. Biol. Evol.*, 5, 331–344.
- Bailey, R.G. (1995). *Description of the Ecoregions of the United States*, 2nd edn. USDA Forest Service, Washington, DC.
- Barracough, T.G. (2015). How do species interactions affect evolutionary dynamics across whole communities? *Annu. Rev. Ecol. Evol. Syst.*, 46, 25–48.
- Bartoli, G., Sarnthein, M., Weinelt, M., Erlenkeuser, H., Garbe-Schönberg, D. & Lea, D.W. (2005). Final closure of Panama and the onset of northern hemisphere glaciation. *Earth Planet. Sci. Lett.*, 237, 33–44.
- Bazzaz, F.A. (1986). *Life History of Colonizing Plants: Some Demographic, Genetic, and Physiological Features*. Springer, New York, pp. 96–110.
- Beaumont, M.A., Zhang, W. & Balding, D.J. (2002). Approximate Bayesian computation in population genetics. *Genetics*, 162, 2025–2035.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecol. Lett.*, 15, 365–377.
- Bintanja, R. & van de Wal, R.S.W. (2008). North American ice-sheet dynamics and the onset of 100,000-year glacial cycles. *Nature*, 454, 869–872.
- Blois, J.L., McGuire, J.L. & Hadly, E.A. (2010). Small mammal diversity loss in response to late-Pleistocene climate change. *Nature*, 465, 771–774.
- Blomberg, S.P., Garland, T. & Ives, A.R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution (NY)*, 57, 717–745.
- Brierley, C.M. & Fedorov, A.V. (2010). Relative importance of meridional and zonal sea surface temperature gradients for the onset of the ice ages and Pliocene-Pleistocene climate evolution. *Paleoceanography*, 25, PA2214, doi:10.1029/2009PA001809.
- Brito, P. & Edwards, S.V. (2009). Multilocus phylogeography and phylogenetics using sequence-based markers. *Genetica*, 135, 439–455.
- Burbrink, F.T. & Castoe, T.A. (2009). Molecular Snake Phylogeography. In *Snakes: Applied Ecology and Conservation*. (eds Mullin, S.J., Seigel, R.A.). Cornell University Press, Ithaca, pp. 38–77.
- Burbrink, F.T., Fontanella, F., Pyron, R.A., Guiher, T.J. & Jimenez, C. (2008). Phylogeography across a continent: the evolutionary and demographic history of the North American racer (Serpentes: Colubridae: *Coluber constrictor*). *Mol. Phylogenet. Evol.*, 47, 274–288.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009). The merging of community ecology and phylogenetic biology. *Ecol. Lett.*, 12, 693–715.
- Chan, Y.L., Schanzenbach, D. & Hickerson, M.J. (2014). Detecting concerted demographic response across community assemblages using hierarchical approximate Bayesian computation. *Mol. Biol. Evol.*, 31, 2501–2515.
- Colleoni, F., Wekerle, C., Näslund, J.-O., Brandefelt, J. & Masina, S. (2016). Constraint on the penultimate glacial maximum Northern Hemisphere ice topography (≈ 140 kyrs BP). *Quat. Sci. Rev.*, 137, 97–112.
- Comes, H.P. & Kadereit, J.W. (1998). The effect of quaternary climate changes on plant distribution and evolution. *Trends Plant Sci.*, 3, 432–438.
- Congdon, P. (2001). *Bayesian statistical modelling*. John Wiley & Sons, Chichester, West Sussex.
- Davis, M.B. (1983). Quaternary history of deciduous forests of Eastern North America and Europe. *Ann. Mo. Bot. Gard.*, 70, 550–563.
- Diamond, J.M. & Case, T.J. (1986). *Community Ecology*. Harper & Row, New York.
- Drummond, A.J., Rambaut, A., Shapiro, B. & Pybus, O.G. (2005). Bayesian coalescent inference of past population dynamics from molecular sequences. *Mol. Biol. Evol.*, 22, 1185–1192.
- Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.*, 29, 1969–1973.
- Edwards, S.V. & Beerli, P. (2000). Perspective: gene divergence, population divergence, and the variance in coalescence time in phylogeographic studies. *Evolution (NY)*, 54, 1839–1854.
- Ferris, C., King, R.A. & Hewitt, G.M. (1999). Isolation within species and the history of glacial refugia. *Mol. Syst. Plant Evol.*, 57, 20–34485.
- Fontanella, F.M., Feldman, C.R., Siddall, M.E. & Burbrink, F.T. (2008). Phylogeography of *Diadophis punctatus*: extensive lineage diversity and repeated patterns of historical demography in a trans-continental snake. *Mol. Phylogenet. Evol.*, 46, 1049–1070.
- Garland, T., Dickerman, A.W., Janis, C.M. & Jones, J.A. (1993). Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.*, 42, 265–292.
- Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (2003). *Bayesian Data Analysis*. Chapman & Hall/CRC, Boca Raton, FL.
- Gillespie, A.R., Porter, S.C. & Atwater, B.F. (2004). *The Quaternary Period in the United States. Developments in Quaternary Science*. Elsevier, Amsterdam, Netherlands.
- Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010). A framework for community interactions under climate change. *Trends Ecol. Evol.*, 25, 325–331.
- Guiher, T.J. & Burbrink, F.T. (2008). Demographic and phylogeographic histories of two venomous North American snakes of the genus *Agkistrodon*. *Mol. Phylogenet. Evol.*, 48, 543–553.
- Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. (2008). GEIGER: investigating evolutionary radiations. *Bioinformatics*, 24, 129–131.
- Harpending, H.C. (1994). Signature of ancient population growth in a low-resolution mitochondrial DNA mismatch distribution. *Hum. Biol.*, 66, 591–600.
- Haug, G.H., Sigman, D.M., Tiedemann, R., Pedersen, T.F. & Sarnthein, M. (1999). Onset of permanent stratification in the subarctic Pacific Ocean. *Nature*, 401, 779–782.
- Hays, J.D., Imbrie, J. & Shackleton, N.J. (1976). Variations in the Earth's orbit: pacemaker of the ice ages. *Science*, 194, 1121–1132.
- Hewitt, G. (2000). The genetic legacy of the Quaternary ice ages. *Nature*, 405, 907–913.
- Hewitt, G.M. (2004). Genetic consequences of climatic oscillations in the Quaternary. *Phil. Trans. R. Soc. Lond. Ser. B. Biol. Sci.*, 359, 183–195.
- Ho, S.Y.W. & Shapiro, B. (2011). Skyline-plot methods for estimating demographic history from nucleotide sequences. *Mol. Ecol. Resour.*, 11, 423–434.
- Hofreiter, M. & Stewart, J. (2009). Ecological change, range fluctuations and population dynamics during the pleistocene. *Curr. Biol.*, 19, R584–R594.

- Hung, C.-M., Drovetski, S.V. & Zink, R.M. (2013). Multilocus test of the absence of mtDNA phylogeographic structure in a widespread wader, the Common Sandpiper (*Actitis hypoleucos*). *J. Ornithol.*, 154, 1105–1113.
- Hurst, G.D.D. & Jiggins, F.M. (2005). Problems with mitochondrial DNA as a marker in population, phylogeographic and phylogenetic studies: the effects of inherited symbionts. *Proc. Biol. Sci.*, 272, 1525–1534.
- Jackson, S.T. & Blois, J.L. (2015). Community ecology in a changing environment: perspectives from the quaternary. *Proc. Natl Acad. Sci.*, 112, 4915–4921.
- Jackson, S.T., Betancourt, J.L., Booth, R.K. & Gray, S.T. (2009). Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proc. Natl Acad. Sci.*, 106, 19685–19692.
- Jackson, S.T., Booth, R.K., Reeves, K., Andersen, J.J., Minckley, T.A. & Jones, R.A. (2014). Inferring local to regional changes in forest composition from Holocene macrofossils and pollen of a small lake in central Upper Michigan. *Quat. Sci. Rev.*, 98, 60–73.
- Jump, A.S. & Peñuelas, J. (2005). Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol. Lett.*, 8, 1010–1020.
- Kleman, J., Jansson, K., De Angelis, H., Stroeve, A.P., Hättestrand, C., Alm, G. *et al.* (2010). North American Ice sheet build-up during the last glacial cycle, 115–21 kyr. *Quat. Sci. Rev.*, 29, 2036–2051.
- Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. (2010). Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annu. Rev. Ecol. Evol. Syst.*, 41, 321–350.
- Lessa, E.P., Cook, J.A. & Patton, J.L. (2003). Genetic footprints of demographic expansion in North America, but not Amazonia, during the Late Quaternary. *Proc. Natl Acad. Sci. USA*, 100, 10331–10334.
- Lurgi, M., López, B.C. & Montoya, J.M. (2012). Novel communities from climate change. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 367, 2913–2922.
- MacDonald, G.M., Bennett, K.D., Jackson, S.T., Parducci, L., Smith, F.A., Smol, J.P. *et al.* (2008). Impacts of climate change on species, populations and communities: palaeobiogeographical insights and frontiers. *Prog. Phys. Geogr.*, 32, 139–172.
- Marshall, S.J., James, T.S. & Clarke, G.K.C. (2002). North American Ice sheet reconstructions at the last glacial maximum. *Quat. Sci. Rev.*, 21, 175–192.
- McCluney, K.E., Belnap, J., Collins, S.L., González, A.L., Hagen, E.M., Nathaniel Holland, J. *et al.* (2012). Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change. *Biol. Rev. Camb. Philos. Soc.*, 87, 563–582.
- McPherson, J.M. & Jetz, W. (2007). Type and spatial structure of distribution data and the perceived determinants of geographical gradients in ecology: the species richness of African birds. *Glob. Ecol. Biogeogr.*, 16, 657–667.
- Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B. *et al.* (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.*, 10, 315–331.
- Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. & Beissinger, S.R. (2008). Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, 322, 261–264.
- Muller, R.A. & MacDonald, G.J. (1997). Spectrum of 100-kyr glacial cycle: orbital inclination, not eccentricity. *Proc. Natl Acad. Sci.*, 94, 8329–8334.
- Northfield, T.D., Ives, A.R., Bertrand, R., Lenoir, J., Piedallu, C., Riofrio-Dillon, G. *et al.* (2013). Coevolution and the effects of climate change on interacting species. *PLoS Biol.*, 11, e1001685.
- Nosil, P. & Feder, J.L. (2013). Genome evolution and speciation: toward quantitative descriptions of pattern and process. *Evolution*, 67, 2461–2467.
- Paradis, E., Claude, J. & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.
- Pearce-Higgins, J.W. & Green, R.E. (2014). *Birds and Climate Change: Impacts and Conservation Responses*. Ecology, Biodiversity and Conservation. Cambridge University Press, Cambridge, U.K.
- Pigot, A.L. & Etienne, R.S. (2015). A new dynamic null model for phylogenetic community structure. *Ecol. Lett.*, 18, 153–163.
- Pyron, R.A. & Burbrink, F.T. (2009). Can the tropical conservatism hypothesis explain temperate species richness patterns? An inverse latitudinal biodiversity gradient in the New World snake tribe Lamprodelphini. *Glob. Ecol. Biogeogr.*, 18, 406–415.
- R Core Team (2015). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rabosky, D.L. (2010). Extinction rates should not be estimated from molecular phylogenies. *Evolution (NY)*, 64, 1816–1824.
- Rahmstorf, S. (2002). Ocean circulation and climate during the past 120 000 years. *Nature*, 419, 207–214.
- Rambaut, A. & Drummond, A.J. (2007). *Tracer v.1.5*. Available at: <http://beast.bio.ed.ac.uk/Tracer>. Last accessed 5 August 2016.
- Ramos-Onsins, S.E. & Rozas, J. (2002). Statistical properties of new neutrality tests against population growth. *Mol. Biol. Evol.*, 19, 2092–2100.
- Raymo, M.E. (1994). The initiation of Northern Hemisphere glaciation. *Annu. Rev. Earth Planet. Sci.*, 22, 353–383.
- Revell, L.J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, 3, 217–223.
- Ricklefs, R.E. (2003). Global diversification rates of passerine birds. *Proc. R. Soc. London Ser. B. Biol. Sci.*, 270, 2285–2291.
- Ricklefs, R.E. (2015). Intrinsic dynamics of the regional community. *Ecol. Lett.*, 18, 497–503.
- Ruane, S., Torres-Carvajal, O. & Burbrink, F.T. (2015). Independent demographic responses to climate change among temperate and tropical milksnakes (Colubridae: Genus *Lampropeltis*). *PLoS ONE*, 10, e0128543.
- Stewart, J.R., Lister, A.M., Barnes, I., Dalén, L., Anderson, L.L., Hu, F.S. *et al.* (2010). Refugia revisited: individualistic responses of species in space and time. *Proc. Biol. Sci.*, 277, 661–671.
- Tajima, F. (1989). Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*, 123, 585–595.
- Tollis, M., Ausubel, G., Ghimire, D. & Boissinot, S. (2012). Multi-locus phylogeographic and population genetic analysis of *Anolis carolinensis*: historical demography of a genomic model species. *PLoS ONE*, 7, e38474.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.*, 12, 1351–1363.
- Vrba, E.S. (1992). Mammals as a key to evolutionary theory. *J. Mammal.*, 73, 1–28.
- Wakeley, J. (2008). *Coalescent Theory: An Introduction*. Roberts & Company Publishers, Greenwood Village.
- Waltari, E., Hijmans, R.J., Peterson, A.T., Nyari, A.S., Perkins, S.L. & Guralnick, R.P. (2007). Locating pleistocene refugia: comparing phylogeographic and ecological niche model predictions. *PLoS ONE*, 2, e563.
- Weinstock, G.M., Robinson, G.E., Gibbs, R.A., Worley, K.C., Evans, J.D., Maleszka, R. *et al.* (2006). Insights into social insects from the genome of the honeybee *Apis mellifera*. *Nature*, 443, 931–949.
- Wong, B.B.M. & Candolin, U. (2015). Behavioral responses to changing environments. *Behav. Ecol.*, 26, 665–673.
- Xue, A.T. & Hickerson, M.J. (2015). The aggregate site frequency spectrum for comparative population genomic inference. *Mol. Ecol.*, 24, 6223–6240.
- Yang, Z. (2014). *Molecular Evolution: A Statistical Approach*. Oxford University Press, Oxford, U.K.

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